Plant Sources of Chinese Herbal Remedies: Laboratory Efficacy, Suppression of *Meloidogyne javanica* in Soil, and Phytotoxicity Assays

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Abstract: Extracts of Chinese herbal medicines from plants representing 13 families were tested for their ability to suppress plant-parasitic nematodes. Effective concentration (EC₅₀ and EC₉₀) levels for 18 of the extracts were determined in laboratory assays with Meloidogyne javanica juveniles and all stages of Pratylenchus vulnus. Efficacy of 17 extracts was tested against M. javanica in soil. Generally, EC₅₀ and EC₉₀ values determined in the laboratory were useful indicators for application rates in the soil. Extracts tested from plants in the Liliaceae reduced galling of tomato by M. javanica and were not phytotoxic. Similarly, isothiocyanate-yielding plants in the Brassicaceae suppressed root galling without phytotoxicity. Other plant extracts, including those from Azadirachta indica, Nerium oleander, and Hedera helix, suppressed root galling but were phytotoxic at the higher concentrations tested. Many of these plant sources have been tested elsewhere. Inconsistency in results across studies points to the need for identification of active components and for determination of concentration levels of these components when plant residues or extracts are applied to soil.

Key words: botanicals, herbal remedies, Meloidogyne javanica, natural products, plant extracts, plant-parasitic nematodes, Pratylenchus vulnus, suppression, toxic effects, phytotoxicity.

Extracts or residues of more than 500 plant species, used alone or in combination, are documented in the literature on Chinese traditional medicine to have activity against helminth and micro-invertebrate pests of humans. In previous studies, we screened 153 candidate medicines, or their plant sources, for effectiveness against plant-parasitic nematodes. Aqueous extracts from 73 of those plant medicinal sources killed either Meloidogyne javanica juveniles or Pratylenchus vulnus (mixed stages), or both, within a 24-hour exposure period. Of 64 remedies reported as antihelminthics, 36 were effective; of 21 classified as purgatives, 13 killed the nematodes; and of 29 indicated as generally effective against pests, 13 killed the nematodes. Sources of effective extracts represented a wide range of plant parts and plant taxa (Ferris and Zheng, 1999; Zheng et al., 1999; Zheng and Ferris, 2001). A unique feature of these plant materials is the extensive information on their uses, physical characteristics, chemical composition, mode of action, and possible side effects as human medicines (e.g., Miao, 1993; Ministry of Public Health, 1985). This background provides the potential for designing plant-parasitic nematode management systems that use materials with different modes of action.

In the present study, we evaluate 18 additional Chinese herbal remedies for their efficacy against plant-parasitic nematodes. These tests, as in the earlier laboratory study (Ferris and Zheng, 1999; Zheng et al., 1999; Zheng and Ferris, 2001), delimit the range of candidate materials for evaluation in soil. The soil tests are a necessary progression because laboratory bioassays are not necessarily indicative of how effective the materials will be in practical application.

MATERIALS AND METHODS

Preparation of plant extracts: Plant extracts were prepared by methodology similar to that described in Ferris and Zheng (1999). Plant materials were air-dried and then soaked in water for 24 hours. They were squeezed through a cotton cloth to separate the aqueous extract from plant residue. For all extracts, the stock concentration was 1 g dry plant material/10 g distilled water; a 100% stock concentration was prepared and diluted to make lower concentrations. Prepared extracts were used immediately in laboratory or greenhouse tests.

Effective concentration studies: The protocol developed by Ferris and Zheng (1999) was used for laboratory determination of the concentration of 18 plant sources (Table 1) that killed 50% (EC₅₀) and 90% (EC₉₀) of M. javanica and P. vulnus. Nematodes were placed in centrifuge tubes with different concentrations of extracted plant material in water. Three replications were prepared for each concentration level. After 24 hours, the tubes were centrifuged, the supernatant fluid removed, distilled water added, and centrifugation was repeated. The supernatant was removed and the remaining nematode-containing fluid was pipeted into a mobility screen floating on distilled water in a 60 × 15-mm petri dish. After 20 hours, the nematodes that had moved through the mobility screen into the petri dish were counted.

Greenhouse experiments: Seventeen plant sources, representing a range of families (Table 2), were tested for efficacy in greenhouse soil tests against M. javanica: Allium cepa, Allium sativum, Armoracia lapathifolia, Asarum sieboldii, Asparagus cochinchinensis, Azadirachta indica, Brucea javanica, Coptis chinensis, Cucurbita pepo, Eugenia caryophyllata, Ginkgo biloba, Hedera helix, Nerium oleander, Ophiopogon japonicus, Sinapis alba, Stemona sessilifolia, and Zingiber officinale. The plant sources chosen had demonstrated suppression of plant-parasitic nematodes in the laboratory and are either commercially available or can be collected from the field.

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Table 1. Effective Concentration₅₀ and Effective Concentration₉₀ values (percentage concentrations, 1 g/10-ml basis) for juveniles of Meloidogyne javanica and mixed stages of Pratylenchus vulnus in extracts of selected plant species.a

	Part	Meloidogyne javanica		Pratylenchus vulnus	
Plant		EC_{50}	EC_{90}	EC50	EC ₉₀
Albizzia julibrissin	Bark	81.9	146.7	89.3	##
Angelica dahurica	Root	50.8	135.6	#b	##
Armoracia lapathifolia	Root	15.7	86.9		
Brucea javanica	Fruit			32.1	##
Cornus officinalis	Fruit	99.1	##"		
Crataegus pinnatifida	Fruit	39.8	147.5		
Cynanchum versicolor	Root	72.7	144.8	135.7	##
Cynanchum stauntoni	Rhizome/root	38.9	##	20110000	1000
Emilia sonchifolia	Whole plant	46.7	##		
Euphorbia hirta	Whole plant	52.4	##	126.9	##
Gentiana scabra	Root	81.7	##	120.5	##
Homalomena occulta	Rhizome			#	##
Houttuynia cordata	Whole plant	103.8	##	-775.	
Ligusticum sinense	Rhizome/root	44.1	144.3		
Lobelia chinensis	Whole plant	155.7	##	76.9	##
Ophiopogon japonicus	Root	20.3	141.4	10.0	n u
Polygonum aviculare	Whole plant	35.2	172.7 ^d		
Portulaca oleracea	Whole plant	79.9	##	194.1	##

^a Data are means of three replicates. Missing data indicate that a combination was not tested. $$^{\rm b}\,\#$$ indicates that estimated EC $_{50}$ level is >2 g/10 ml water and may be

Greenhouse experiments were conducted during 1998 and 1999. Two-week-old tomato seedlings were transplanted into 1.5-liter clay pots filled with a 2:1 sand:loam mix. Tomato plants were allowed to grow for 20 to 30 days, depending on greenhouse conditions. Pots were inoculated with 2,000 (1998) and 4,000 (1999) M. javanica juveniles per pot. In 1998, approximately 1 hour after inoculation, 300 ml extract was applied to the soil surface. Sufficient extract was applied to saturate the soil without causing the excess to leach from the bottom of the pot. An additional 300 ml extract was applied the next day so that each pot received a total of 600 ml. In 1999, a total of 300 ml extract was applied per pot in one application 1 hour after infestation with nematodes. This amount was based on the field capacity of the 2:1 sand/loam mix in the pots. For each extract, three concentrations were evaluated based on laboratory EC50 and EC90 levels determined either in this study or previously reported (Ferris and Zheng, 1999; Zheng and Ferris, 2001). Two controls were included, tomatoes with (+Mj) and without (-Mj)M. javanica; neither received plant extract but did receive equivalent amounts of water. Each concentration of extract was replicated five (1998) or four (1999) times, and the experiments were arranged in completely randomized designs.

The soil in each pot was drip-irrigated twice daily to

field capacity with a 180-N, 42-P, 156-K, 210-Ca, and 100-Mg mg/L nutrient solution. After 8 weeks, tomato plants were harvested, and top, fruit, and root weights and gall index (Daulton and Nusbaum, 1961) were determined.

Data analysis: To standardize extract concentrations experienced by the nematodes in the two experiments, we calculated the amount of dry plant material applied to each pot and adjusted the concentration to the 300 ml water in each pot at field capacity. Exposure concentrations are expressed as g dry plant material per 10 ml soil solution. Gall ratings were converted to percent gall reduction based on 0% gall reduction in the +Mj control. Tomato weights were expressed relative to the weight of the -Mj control.

Data for each medicinal plant source were analyzed separately and expressed as means. When testing of the same plant source was repeated, standardized data from 1998 and 1999 were combined. All data were subjected to analysis of variance with the general linear model (GLM) procedure of SAS (SAS Institute, Cary, NC). Treatment means were separated with Duncan's multiple-range test at P = 0.05. In both laboratory and greenhouse experiments, EC50 and EC90 values were determined for nematode mortality (or reduction in root galling) by probit analysis (SAS Institute, Cary, NC).

RESULTS

Effective concentration studies: In some cases, EC50 and EC90 levels of M. javanica were achieved at relatively low concentrations of the plant extract (e.g., Armoracia lapathifolia) (Table 1). Although 50% mortality of M. javanica was achieved at low concentrations of Ophiopogon japonicus and Polygonum aviculare, much higher concentrations were needed to achieve 90% mortality. Whereas EC50 values for P. vulnus could be calculated through probit analysis for some plant sources, the projected EC90 levels were always greater than 2 g/10 ml water and may be impossible to prepare in aqueous solution.

Greenhouse studies: When extracts were applied to the soil around tomato plants, three types of responses were observed: reduction in M. javanica galling and no reduced plant growth; reduction in M. javanica galling and reduced plant growth; and extreme phytotoxicity. Eight of the plant sources reduced M. javanica galling and were not phytotoxic to tomato plants at the concentrations tested (Table 3). Allium cepa and Asarum sieboldii reduced galling at 1.5 and 1.6 g/10 ml, respectively. For both of these plant sources there was a reduction in galling of tomato of at least 75% at all concentrations (data not shown). At the lowest concentrations applied for the other plant sources, the reduction in galling was 75% for Zingiber officinale, 29% for Ophiopogon japonicus, 36% for Sinapis alba, 57% for Ginkgo

impossible to prepare in aqueous solution.

^{##} indicates that estimated EC90 level is >2 g/10 ml water and may be impossible to prepare in aqueous solution.

EC levels greater than 100% of stock solution concentration are estimated by probit analysis extrapolation.

Taxonomic and growth characteristics of medicinal plants tested for Meloidogyne javanica suppression in soil and phytotoxicity to tomato.

Plant source	Common name	Family	Growth habit	Plant part
Allium cepa L.	Onion	Liliaceae	Herb	Bulb
Allium sativum L.	Garlic	Liliaceae	Herb	Clove
Armoracia lapathifolia Gilib.	Horseradish	Brassicaceae	Herb	Root
Asarum sieboldii Miq.	Wild ginger	Aristolochiaceae	Herb	Whole plant
Asparagus cochinchinensis Merr.	Cochinchinese asparagus	Liliaceae	Herb	Root
Azadirachta indica Adr. Juss.	Neem	Meliaceae	Tree	Bark
Brucea javanica Merr.		Simaroubaceae	Shrub	Fruit
Coptis chinensis Franch.	Coptis	Ranunculaceae	Herb	Root
Cucurbita pepo L.	Pumpkin	Cucurbitaceae	Vine	Seed
Eugenia caryophyllata Thunb.	Dovetree	Myrtaceae	Tree	Clove
Ginkgo biloba L	Maidenhair tree	Ginkgoaceae	Tree	Fruit
Hedera helix L.	English Ivy	Araliaceae	Vine	Whole plant
Nerium oleander L.	Oleander	Apocynaceae	Shrub	Leaf
Ophiopogon japonicus KerGawl.	Dwarf lilyturf	Liliaceae	Herb	Root
Sinapis alba L.	White mustard	Brassicaceae	Herb	Seed
Stemona sessilifolia Miq.	Stemona	Stemonaceae	Herb	Root
Zingiber officinale Rosc.	Ginger	Zingiberaceae	Herb	Stem

biloba, 84% for Coptis chinensis, and 56% for Allium sativum.

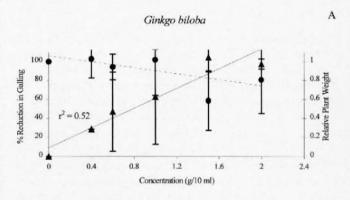
There was a range of response patterns of M. javanica galling to different medicinal plant sources (Fig. 1). For example, the percentage gall reduction increased proportional to the concentration of Ginkgo biloba extract $(r^2 = 0.52; P = 0.001)$. Relative tomato weight did not decrease over this concentration range (P = 0.05). While relative plant weight did not decrease with increasing concentrations of Sinapis alba (P = 0.02), the effect asymptote, at which there was no further reduction of galling, was reached at different concentrations than for Ginkgo biloba.

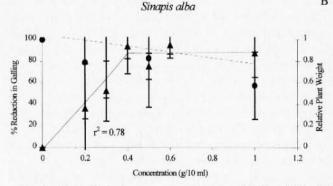
Eight of the plant sources tested reduced M. javanica galling but were phytotoxic to tomato (Table 4). Azadirachta indica, Cucurbita pepo, and Hedera helix reduced galling at least 90% at 1.6, 1.6, and 2.0 g/10 ml, respectively. Azadirachta indica and Cucurbita pepo were also phytotoxic at these concentrations, while Hedera helix was phytotoxic to tomato at >2.0 g/10 ml. Armoracia lapathifolia and Nerium oleander were phytotoxic at 0.4 and >2.0 g/10 ml, respectively, and killed the plants.

Lowest concentration of plant extract added to soil (g-per-10-ml basis)a resulting in Meloidogyne javanica gall reduction where the extract was not phytotoxic to tomato.

Plant source	Gall reduction (g/10 ml) ^b	
Allium cepa	1.5	
Allium sativum	0.15	
Asarum sieboldii	1.6	
Coptis chinensis	0.4	
Ginkgo biloba	1.0	
Ophiopogon japonicus	0.2	
Sinapis alba	0.2	
Zingiber officinale	1.4	

Armoracia lapathifolia reduced galling by 77% at 0.15 g/10 ml, and Nerium oleander reduced galling by 56% at 1.5 g/10 ml. A greater range of plant extract concentrations was tested for the other plant sources that were phytotoxic to tomato. At 0.3 g/10 ml of Asparagus cochinchinensis there was a 75% reduction in galling, at 1.0 g/10 ml of Stemona sessilifolia there was a 59% reduction





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Fig. 1. The effect of extract concentration of Ginkgo biloba (A) and Sinapis alba (B) on % reduction in galling by Meloidogyne javanica (triangles) and relative plant weight (circles) of tomato. Vertical bars indicate standard error. Dashed line represents tomato phytotoxicity; solid line represents nematode galling.

 ^a g dry plant material per 10 ml soil solution.
 ^b Lowest concentration at which gall reduction occurs (Point C₁ in Fig. 3).

Lowest concentration of plant extract added to soil (g-per-10-ml basis)" resulting in Meloidogyne javanica gall reduction and reduction in growth of tomato.

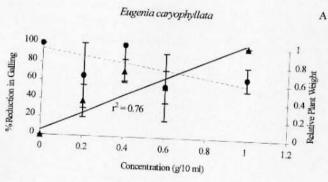
Plant source	Gall reduction (g/10 ml) ^b	Phytotoxicity (g/10 ml) ^c
Armoracia lapathifolia Asparagus cochinchinensis	0.15	0.4
Azadirachta indica	0.3	0.6
Cucurbita pepo	1.6 1.6	>2.0
Eugenia caryophyllata	0.2	1.6
Hedera helix Nerium oleander	2.0	0.6 >2.0
Stemona sessilifolia	1.5	>2.0
" g dry plant material pur 10	1.0	>2.0

g dry plant material per 10 ml soil solution.

Lowest concentration at which phytotoxicity occurs (Point C2 in Fig. 3).

in galling, and at 0.2 g/10 ml of Eugenia caryophyllata there was a 38% reduction in galling (Table 4).

Over the range of concentrations tested for Eugenia caryophyllata and Stemona sessilifolia, the asymptote was reached at different points (Fig. 2). There was a linear relationship between percent reduction in galling and concentration up to 1.0 g/10 ml for Eugenia caryophyllata ($r^2 = 0.77$). At higher concentration of this plant source (2.0 g/10 ml), tomato plants died. For Stemona sessilifolia the percent reduction in galling increased up to $1.25 \text{ g}/10 \text{ ml (r}^2 = 0.88)$. Brucea javanica was phytotoxic at all concentrations applied (data not shown).



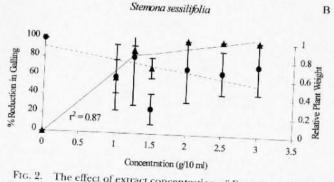


Fig. 2. The effect of extract concentration of Eugenia caryophyllata (A) and Stemona sessilifolia (B) on % reduction in galling by Meloidogyne javanica (triangles) and relative plant weight (circles) of tomato. Vertical bars indicate standard error. Dashed line represents tomato phytotoxicity; solid line represents nematode galling.

Tomato plants died within a few days of the application of this plant source.

In the EC50 and EC90 analyses for M. javanica in soil (Table 5), all concentrations of Allium cepa, Armoracia lapathifolia, Asarum sieboldii, Azadirachta indica, Cucurbita pepo, and Hedera helix reduced root galling by more than 50%. The soil EC50 for Allium sativum, Asparagus cochinchinensis, and Coptis chinensis could not be determined because the percentage gall reduction across concentrations was not consistent. All concentrations tested below 1.0 g/10 ml for Ginkgo biloba were not significantly different from the control. Zingiber officinale was the only plant source that did not reduce galling by 90% at any concentration tested (Table 5). Armoracia lapathifolia and Nerium oleander killed plants at higher concentrations tested; therefore, the EC90 could not be determined.

DISCUSSION

This study continues a progression of experiments to determine the efficacy, as aqueous extracts, of plant sources of Chinese herbal remedies against plantparasitic nematodes. The initial laboratory evaluation of 153 plant sources reported in Ferris and Zheng (1999) was by direct observation and measures of effects on nematode motility. Of these 153, the EC_{50} and EC₉₀ have been determined for 43 plant sources—25 reported in Ferris and Zheng (1999) and 18 reported here.

The extracts varied in their efficacy at different concentrations. The selection of a stock solution concentration of 1 g plant material/10 ml water provides no quantifiable/quantitative measure of active components and therefore is not useful as a standard for com-

TABLE 5. Summary of Effective Concentration₅₀ and Effective Concentration₉₀ values (g-per-10-ml basis)^a for Meloidogyne javanica

Plant source	Plant part	ECen	EC
Allium cepa Allium sativum Armoracia lapathifolia Asarum sieboldii Asparagus cochinchinensis Azadirachta indica Coptis chinensis Cucurbita pepo Eugenia caryophyllata Ginkgo biloba Hedera helix Nerium oleander	Bulb Clove Root Whole plant Root Bark Root Seed Clove Fruit Whole plant	EC ₅₀ ** ** <0.15 <1.6 ** 1.6 ** <1.6 0.4 1.0 2.0	1.6 0.3 ** 2.0 1.0 2.0 1.6 1.6 1.0 2.0 2.0
Ophiopogon japonicus linapis alba lemona sessilifolia lingiber officinale	Root Seed Root Stem	1.5 0.4 0.3 1.0	1.0 0.4 2.0

g dry plant material per 10 ml of soil solution.

Not able to determine based on data.

b Lowest concentration at which gall reduction occurs (Point C₁ in Fig. 3).

paring the relative efficacy of sources. Where the estimated EC_{90} levels were >200% of stock solution concentration (e.g., Gentiana scabra and Lobelia chinensis), the data are not presented because, for most of these plant materials, it was not possible to prepare stock solution concentrations containing more than 2 g plant material/10 ml water. In cases where the EC_{90} level is much greater than the EC_{50} level, it may be difficult to obtain enough material to reach the EC_{90} level in field applications. This may be the case in obtaining enough bark or fruit material for Albizzia julibrissin and Crataegus pinnatifida, respectively.

All of the 17 plant sources tested in greenhouse soil experiments reduced root galling by *M. javanica*. For the majority of plant sources tested, EC₅₀ and EC₉₀ levels determined in the laboratory and in soil were similar. This demonstrates the value of screening plant materials in the laboratory before undertaking time-consuming and costly greenhouse experiments. In addition to eliminating ineffective material, EC levels can be determined in water as a basis for selection of concentrations for soil tests.

All of the plant sources tested from the family Liliaceae reduced nematode galling and were not phytotoxic to tomato. The nematicidal properties of Allium sativum and Asparagus cochinchinensis have been reported (Sukul, 1992). The suppression of nematodes may be due to the active components glucoside and asparagusic acid in Asparagus spp. (Sukul, 1992) and allicin in Allium sativum (Gupta and Sharma, 1993). In contrast, methanol extracts of Allium sativum bulbs and Allium cepa leaves were inactive against Bursaphelenchus xylophilus (Mackeen et al., 1997). While we saw no phytotoxicity to tomato by Allium sativum, okra (Abelmoschus esculentus) receiving aqueous extracts of Allium sativum died within 24 hours (Sukul et al., 1974).

Armoracia lapathifolia and Sinapis alba, both in the family Brassicaceae, reduced nematode galling in this study. The effectiveness of extracts of plants in the family Brassicaceae in suppressing plant-parasitic nematodes is well documented (Jing and Halbrendt, 1994; Potter et al., 1998). Isothiocyanates, or related compounds, produced by the hydrolysis of glucosinolates are purported to be responsible for the death or inhibition of plant-parasitic nematodes.

Aqueous extracts of Zingiber officinale decreased root galling by M. incognita and were mildly phytotoxic to okra (Sukul et al., 1974). Mackeen et al. (1997) found that methanol extracts of Zingiber officinale rhizomes were not active against B. xylophilus. In this study, Zingiber officinale reduced the percent root galling across the range of concentrations tested and was not phytotoxic to tomato.

Azadirachta indica, or neem, has been studied extensively for its effects against plant-parasitic nematodes. Kaempterol and myricetin are the chemical components thought to be responsible for the nematicidal

properties (Qamar et al., 1989). Leaf extracts of Azadirachta indica were toxic to Helicotylenchus dihystera and significantly increased the growth of tomato plants (Firoza and Maqbool, 1996). In our study, Azadirachta indica was phytotoxic to tomato at the highest concentration applied. Pradhan et al. (1989) demonstrated that tomato seedling root-dips with Azadirachta indica were more effective than soil treatment in controlling M. incognita.

From the latex-yielding plants, we tested *Nerium ole*ander, family Apocynaceae. Fresh latex obtained from *Nerium oleander* was toxic to juveniles and reduced egg hatch of *M. javanica* (Zureen and Khan, 1984). In our studies, while *Nerium oleander* suppressed *M. javanica*, it was also phytotoxic at the highest concentration applied.

In the family Araliceae, we tested *Hedera helix*. Plants in this family are known to contain polyacetylenes, specifically falcarinone in *Hedera helix*. The antifungal activity of the polyacetylenes has been documented (Hansen and Boll, 1986). Our study demonstrated that *Hedera helix* suppressed *M. javanica* but was phytotoxic at the highest concentration applied.

Unless the mode of action is very specific, any plant component eliciting an effect on nematode physiological systems is likely also to have an effect on plant physiological systems. However, phytotoxicity of a plant extract is not, a priori, a basis for rejecting its potential utility in nematode management. Many antibiotics, for example, are toxic to the patient if administered at levels above a specified dosage. In these studies, we have determined the concentration at which the extract becomes effective against nematodes in soil (Fig. 3, point C_1), the concentration at which it becomes phytotoxic to plants (point C_2), and the concentration at which some specified proportion of the nematode population is affected—say >95% (E₉₅) (point C_3). The optimum concentration of the extract is that at which

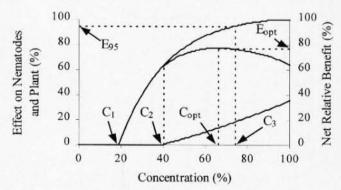


FIG. 3. Conceptual model for assessing field application potential of plant extracts and residues in nematode management. C_1 = concentration at which the extract becomes effective against nematodes in soil; C_2 = concentration at which it becomes phytotoxic to plants; C_3 = concentration at which a specified proportion of the nematode population is affected; $C_{\rm opt}$ = concentration of the material at which the "benefit" is maximized; $E_{\rm opt}$ = the optimum benefit.

the "benefit" (Eopt, the difference between positive effects on nematode viability and negative effects on plant health) is maximized (point Copt). The most desirable plant extracts are those with very specific modes of action against the target organisms and no phytotoxic effects. We define these as Category A materials. In Category B are plant extracts for which C2 > C3, that is, significant mortality of the nematode population occurs at concentrations below phytotoxic levels. In Category C are those materials for which $C_2 > C_1$ and C_{opt} > C2, that is, there is some benefit to application of lower concentrations. Such materials might have application when used in combination with other plant sources to elicit synergistic effects. Category D materials are those for which C₁ > C₂. Category D materials appear to have little potential in nematode management unless, similar to certain fumigant nematicides, they can be applied early and dissipate prior to planting. In that case, it may be possible to increase the difference in concentration between C2 and C1, and to maximize Eoot. We characterize the plant extracts screened in our soil tests according to these criteria (Tables 3 and 4).

In laboratory and greenhouse studies, plant sources were screened for their ability to suppress plantparasitic nematodes. However, the active components and their concentrations in the aqueous extracts of the plant sources are not known. Further, solvent-based extracts (e.g., methanol) of these plant materials would undoubtedly contain different range and concentrations of active components. Aqueous extracts were used in these studies in the belief that they most closely resemble the chemistry of soil-incorporated plant residues. Although we have demonstrated that many plant sources will suppress M. javanica in a soil environment, it is recognized that efficacy may vary due to many factors (e.g., plant age, time of collection, location, application technique, soil type). Future research in this area should focus on the direct testing of specific plant components and their suppressiveness against plantparasitic nematodes.

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